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A Comparison of Length and Voltage in the Electric Eel, *Electrophorus electricus* (Linnaeus).

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(Text-figures 1-5).

In observations on a number of electric eels, *Electrophorus electricus* (Linnaeus), made during the last few years, it appears that there is a voltage-length relationship which is more or less constant for eels of any given length, and which differs between length groups, the shorter eels having a higher voltage value per unit length, the longer fish a lesser voltage. While there are individual differences between one fish and another of identical length, these are within the general range of the group.

Since the fish depends entirely upon its electricity for protection against enemies and for securing food, it seems likely that the smaller ones must develop a sufficiently high voltage early in life to be effective, but once this effective voltage is achieved, there is no need for it to increase with increasing length.

It has not been possible for us to measure eels of very small size, so that we make no conjectures for these, but we were recently afforded the opportunity of making measurements on 59 eels, secured in September, 1944, for purposes other than this paper. The lengths of these fish ranged from 34.5 cm. to 191 cm.

Since these fish were freshly caught before the first group of measurements was made, and had been in captivity for several months when the second measurements were made, it is as well to point out that we have found no significant differences in voltage between fish kept in tanks in New York and fish which were in their native waters in Brazil.

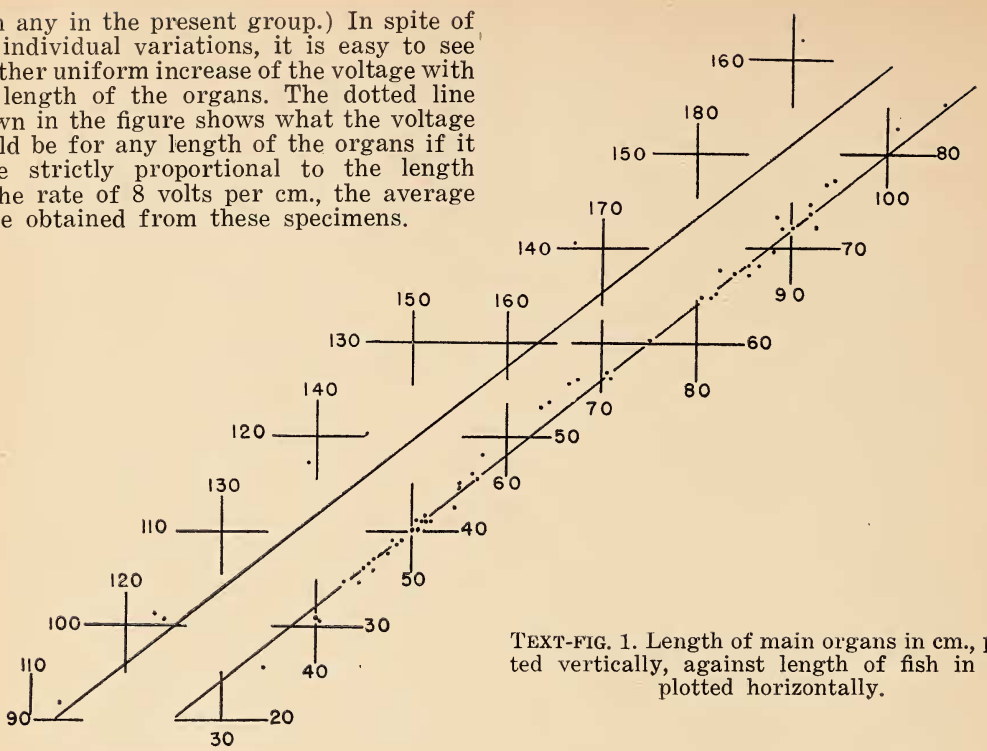
Some of the measurements were made in October, 1944, and the rest in January, 1945. The fish employed at the earlier dates were not kept segregated afterwards, and it is therefore likely that some of them were among those measured at the later date. This is not a disadvantage, however, since a good deal of growth took place between the two dates, and the purpose of the measurements was to learn how the electrical characteristics of the fish are changed by growth.

Because only a limited time was available for the observations and it was desired to make them on a large number of specimens, only the simplest measurements were made. One of these was the measurement of the length of the main electric organs.

The anterior end of these organs is just behind the very soft tissue of the visceral cavity and is easily discernible through the skin if a slight pressure is exerted. The posterior end of the organs is at the tip of the tail. Consequently it was quite easy to determine the length of these organs and compare it with the length of the fish. The comparison is shown in Text-fig. 1. It will be seen that for any one length of the fish there is little variation in the length of the organs. Also there is a remarkable uniformity in the ratio of the length of the organs to the length of the fish. The average value of this ratio is 0.80, and the average deviation is less than 2 per cent.

By connecting a cathode-ray oscillograph to electrodes at the ends of the main organs, the maximum voltage developed in the discharge of these organs was measured for each fish. The fish was out of water and no current was drawn from the organs except that flowing in circuits closed within the body of the fish. Here the individual variations are much more marked than in the length of the organs. Also the relation of the maximum voltage to the length of the organs, instead of being regular, shows a rather abrupt change as the organs attain a length of about 50 cm. The measurements on the smallest twenty-five specimens, those with electric organs under this length, are shown in Text-fig. 2. (There is shown also, by a dot, a measurement made by one of us some years ago in Brazil on a specimen smaller

than any in the present group.) In spite of the individual variations, it is easy to see a rather uniform increase of the voltage with the length of the organs. The dotted line drawn in the figure shows what the voltage would be for any length of the organs if it were strictly proportional to the length at the rate of 8 volts per cm., the average value obtained from these specimens.



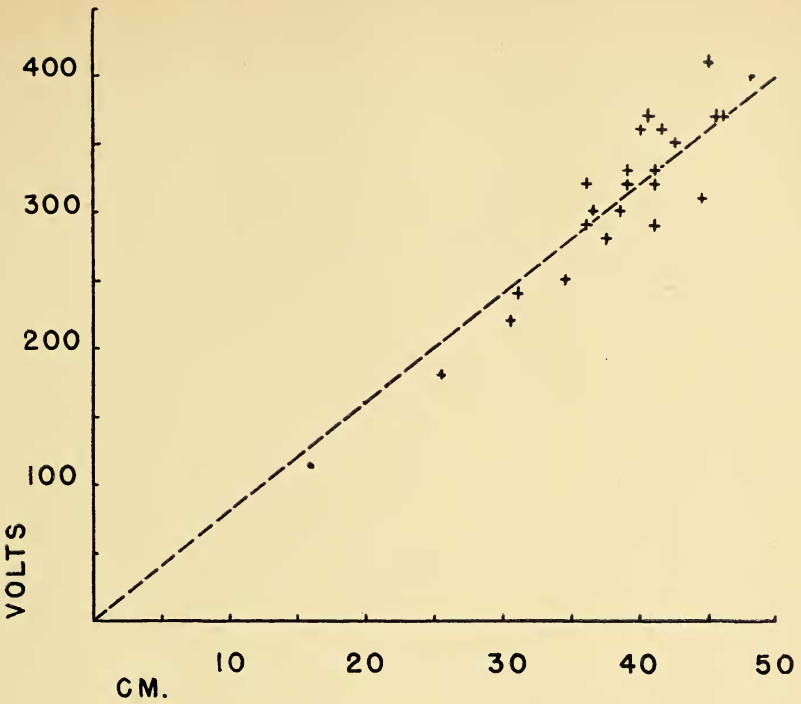
TEXT-FIG. 1. Length of main organs in cm., plotted vertically, against length of fish in cm., plotted horizontally.

If this rate were maintained at all lengths, the largest fish in these observations, with organs 162 cm. long, would have a maximum voltage of almost 1,300 volts. Actually the maximum voltage of this fish was only 340 volts. The measurements made on the whole group of larger fish, shown in Text-fig. 3, do not indicate an increase in voltage with increasing length of the organs. The voltages regardless of length seem to be randomly scattered around their average value, 370 volts. The highest voltage measured, 550 volts, was produced by almost the smallest fish of the group. Evidently, then, the increase of voltage with growth shown by the observations on the group of smaller fish stops, apparently with some suddenness, when a certain length is attained. The fact that the individual variations are markedly greater among the larger fish suggests that the greatest voltage is attained at different lengths in different specimens.

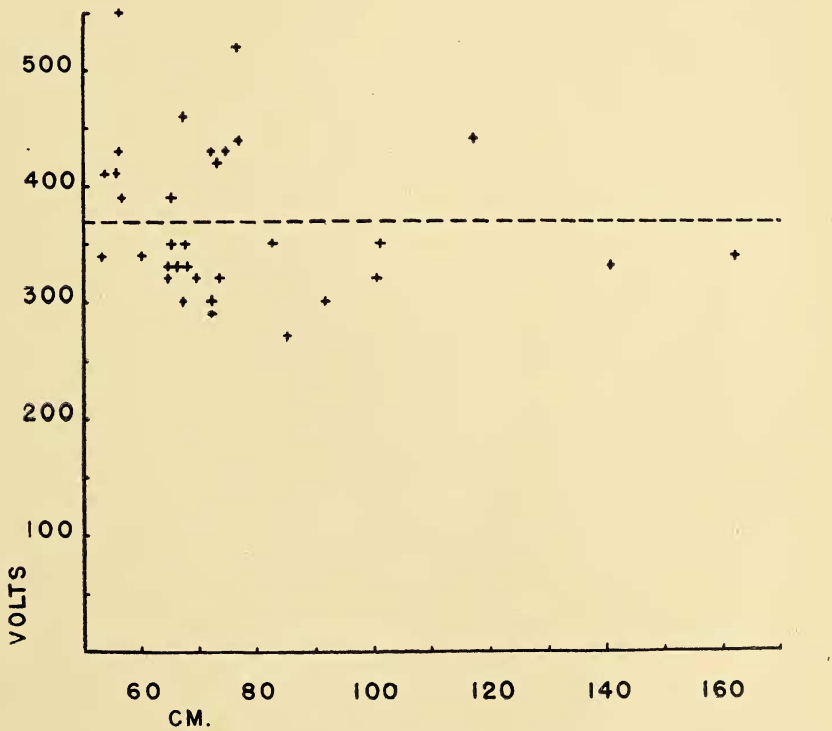
Though this is the most extensive comparison of the lengths and voltages of electric eels which we have been able to make, we have observed over a number of years that the voltages of large fish bore to those of small fish a ratio less than the ratio of their lengths. At one time we ventured the opinion that the limiting factor in the increase of voltage with length was the speed at which the impulse runs along the electric organs (1). If, during the discharge of the anterior part of the organs, the impulse should traverse only a certain fraction of their length, then the parts posterior to this fraction would only prolong the discharge without increasing the voltage. The speed was found to have a value of the right order to make this explanation seem plausible. However, measurements of voltage between electrodes near together at the anterior end of the organs show that the factor which limits the increase of voltage with length is actually something else than the speed of the impulse.

These measurements are shown in Text-figs. 4 and 5, in which the maximum voltages per unit length at the anterior end of the organs are plotted against the length of the organs. For the smaller fish, as shown in Text-fig. 4, the voltage per cm. shows no systematic change with the length of the organs. For the larger fish, on the other hand, the voltage per cm. shows a decrease with increasing length discernible despite the wide individual variations.

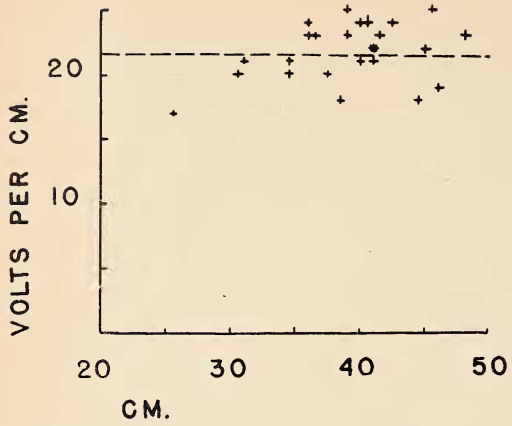
Now, these measurements were made with electrodes 5 cm. apart. The speed of the impulse at the anterior end of the organs is of the order of 2 meters per millisecond. Hence the time lag in 5 cm. would be only about .02 or .03 millisecond, roughly 100 times less than the duration of the discharge. Thus the time lag can have no appreciable effect on the voltage measured in so short a length of the organs. Nevertheless the voltage per cm. is less in the large fish than in those with organs less than 50 cm. long, and it is less



TEXT-FIG. 2. Maximum voltage of main organs against length of organs, smaller fish.



TEXT-FIG. 3. Maximum voltage of main organs against length of organs, larger fish.



TEXT-FIG. 4. Maximum voltage per cm, at anterior end of main organs, against length of organs, smaller fish.

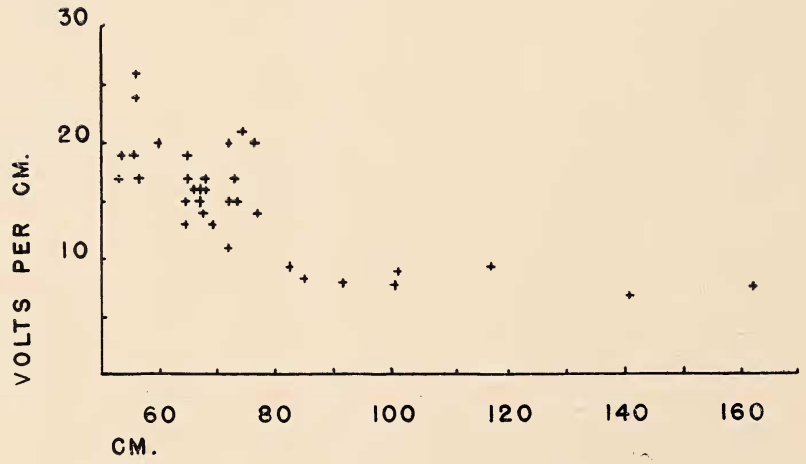
in a proportion about enough to account for the observed independence of voltage and length among the larger fish.

The individual variations are large enough to allow still the possibility that the speed of the impulse may contribute something to the limitation of voltage, but there is no positive evidence that it does. If there is no such effect, it may be that the speed of the impulse increases with the growth of the fish and so has the same effect on the voltage in long fish as in short ones. The speed has not been measured in enough specimens to be certain on this point, though the few measurements made show the greater speed in the longer fish. (1)

It will be recalled that when the voltage was measured between the ends of the organs, the average voltage per unit length among the smaller fish, in which it was highest, was found to be 8 volts per cm. At the anterior end of the organs, however, the average voltage per unit length was found to be 22 volts per cm., almost three times as high as for the organs as a whole. This variation of the voltage per cm. along the length of the organs has been observed before and correlated with the variation of the number of layers of electroplaxes per cm. in series along the organ (2, 3). The voltage per electroplax layer was found to be roughly uniform along the organs and to have in several different fish the same order of magnitude, about 0.14 volt. It seems reasonable, therefore, to ascribe the differences in the voltage per cm. found in the group of longer fish mainly to the same cause. It may be supposed that when the organs attain a length around 50 cm., further growth takes place not by an increase in the number of electroplax layers but by an increase in the thickness of the layers. This supposition is confirmed by observations on a few specimens in which, in connection with other experiments, the number of layers per cm. was counted in specimens of different lengths (4).

In this connection it may be mentioned that Cox and Breder, in comparing embryo and adult specimens of the electric ray, *Narcine brasiliensis* (Ölfers), found that the enlargement of the electroplaxes would account for most of the growth of the electric organs (5).

If it be supposed that among the electric eels with organs less than 50 cm. in length the voltage per electroplax layer also does not appreciably change with growth, then it must be concluded, in order to account for the increase in the voltage of the whole organs, that growth up to this length takes place by an increase in the number of electro-



TEXT-FIG. 5. Maximum voltage per cm. at anterior end of main organs, against length of organs, larger fish.

plax layers. If this is true, so that there is a radical change in the process of growth around this length, then it may be somewhat surprising that this change is not accompanied by a change in the ratio of the length of the organs to the length of the fish. As was shown in Text-fig. 1, this ratio remains remarkably constant. An alternative explanation would be that the voltage per electroplax layer increases in the early stages of growth without an increase in the number of layers. On this explanation, however, it would be surprising that the voltage of the whole organs is so nearly proportional to the length among the smaller fish as it is found to be and that the voltage per cm. at the anterior end is so nearly uniform. It seems to us more likely, on the present evidence, that the voltage per electroplax layer does not depend much, if at all, on the length of the organs, and that the early growth is mainly an increase in the number of electroplax layers, while the later growth is mainly an increase in their thickness. Of course it would be possible, by dissecting the organs of enough specimens of different sizes, to determine definitely the process of growth, but the question does not seem at present to have enough importance to justify the sacrifice of the fish that this would require.

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